

# SPECIES DISJUNCTIONS IN *LARREA*: EVIDENCE FROM MORPHOLOGY, CYTOGENETICS, PHENOLIC COMPOUNDS, AND SEED ALBUMINS<sup>1</sup>

J. H. HUNZIKER,<sup>2</sup> R. A. PALACIOS,<sup>2</sup> AMALIA G. DE VALESÍ<sup>2</sup>  
AND LIDIA POGGIO<sup>2</sup>

*Larrea divaricata*, the "creosote bush," is often regarded as the most drought tolerant higher plant in North America (Barbour, 1969; Morello, 1955). It is probably a single species having an enormous disjunct distribution. In North America it extends from the State of Nevada to the State of Hidalgo in Mexico, where it is called "gobernadora" on account of its dominance in the natural vegetation (Fig. 1). In South America it occurs in several isolated places in Peru (Ica, Nazca, Chuquibamba, Moquegua), in Bolivia (Tarija), and in Chile (Atacama, Concepción). In Argentina it is called "jarilla," and it extends from Salta in the North to North Patagonia (Chubut) (Fig. 2). As pointed out by Barbour the disjunction reaches 36 degrees latitude, that is, nearly 4,000 km (Barbour, 1969).

The question that immediately arises, when considering such an extense distribution is whether we are dealing with a single species or at least two vicariant species: *Larrea tridentata* (North America) and *L. divaricata* (South America).

How much have these populations diverged since they became separated? Typical *Larrea divaricata* was described from Mendoza, Argentina, South America, and the North American taxon has been named *L. tridentata*. Morphologically, they can easily be separated by the form of the stipules, the North American populations having acute while the South American ones have obtuse stipules. They could be distinguished, therefore, as different subspecies as done recently by Felger and Lowe (1970) who recognize *L. divaricata* Cav. subsp. *divaricata* for the South American subspecies and its ecotypes and subsp. *tridentata* (Sesse & Moc. ex DC.) Felger & Lowe for the North American subspecies and its ecotypes.

## BIOSYSTEMATICS OF THE GENUS *LARREA*

A brief consideration of the biosystematics of the genus will help us to have an idea of the degree of morphological diversity and the genomic differentiation of

---

<sup>1</sup> The authors wish to express their gratitude to several persons that in one way or another helped their research. Mrs. Vilma B. de Fernández performed the protein electrophoresis experiments; Miss Aída De Gregorio made part of the cytological preparations; Dr. J. Morello gave us some data on the present day distribution of *L. divaricata* in Santiago del Estero, Argentina, Dr. J. Rzedowski and Dr. Otto T. Solbrig collected seed samples in the field; Dr. Tien Wei Yang very generously supplied us with many seed samples identified insofar as chromosome number is concerned. Financial support through a National Science Foundation (U.S.A.) grant to Dr. O. T. Solbrig and two grants from the Consejo Nacional de Investigaciones Científicas y Técnicas to the senior author is acknowledged.

<sup>2</sup> Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Ciudad Universitaria, Buenos Aires, Argentina.

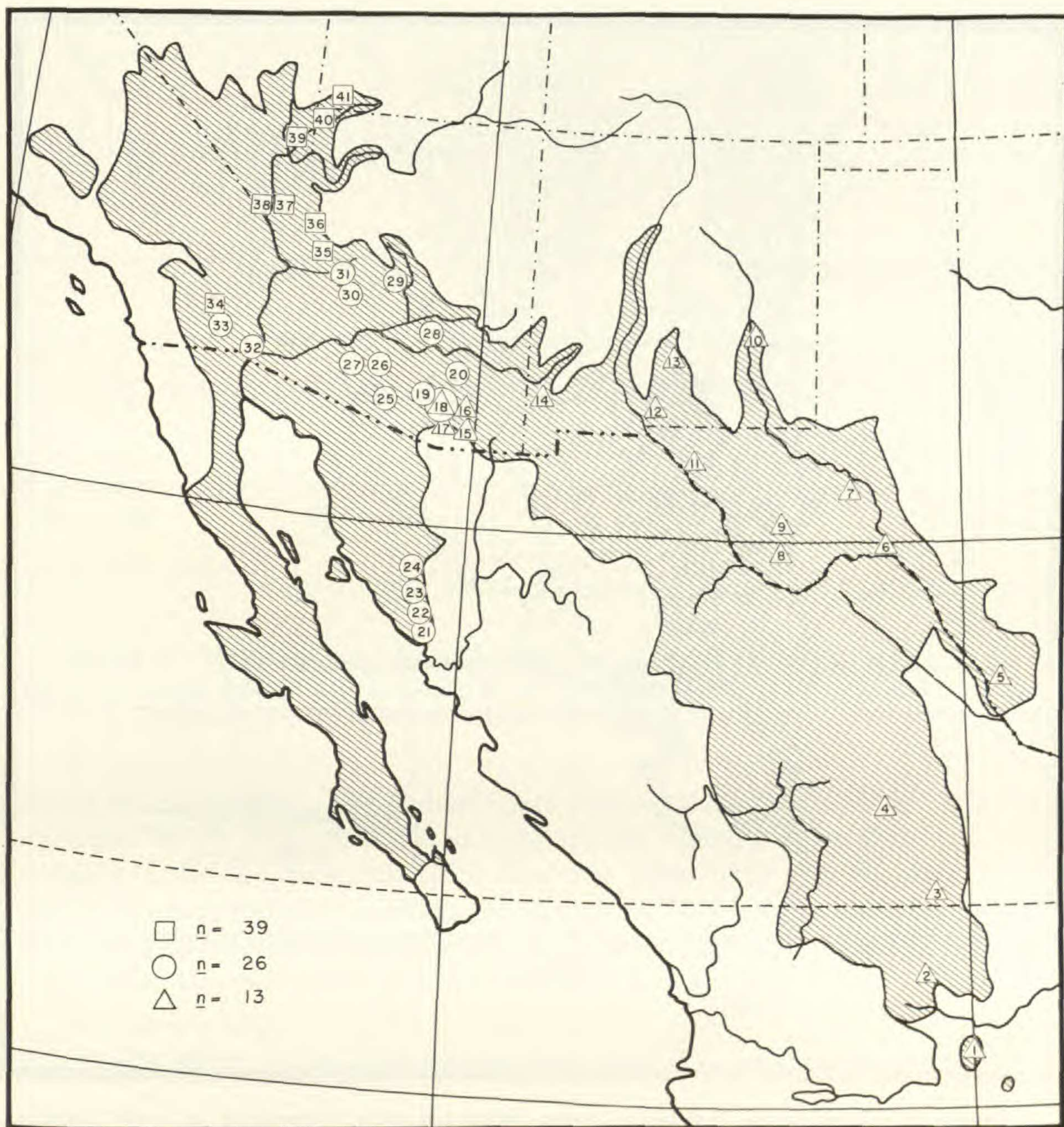


FIGURE 1. Chromosome numbers of creosote bush populations in North America (*Larrea divaricata* subsp. *tridentata*). Diploid populations 1–17 occur in the Chihuahuan Desert and adjacent desert grassland. Tetraploid populations 19–33 are situated in the Sonoran Desert. Hexaploid populations 35–41 are located in the Mojave Desert. Shaded area shows the contemporary distribution of *Larrea divaricata* subsp. *tridentata* in North America. Reproduced from Yang (1970) by kind permission of the author.

the species, the center of species diversity, the age of some species, and the possible patterns of migration.

Table 1 summarizes some of the characteristics of the five taxa of the genus *Larrea* and their geographic distribution. The multifoliolate species having small petals and many leaflets are supposed to be representatives of a more primitive group, since most species of the other genera in the family Zygophyllaceae are multifoliolate. The bifoliolate species would represent a more specialized and recent group. All species have acute (or nearly so) stipules except South American *L.*



FIGURE 2. Distribution of diploid *Larrea divaricata* subsp. *divaricata* in South America. The triangles indicate localities where chromosome counts ( $n = 13 \text{ II}$ ) have been made. (Base map copyright University of Chicago.)

*divaricata* subsp. *divaricata* which has obtuse stipules. North American *L. divaricata* subsp. *tridentata* has acute stipules (Fig. 3) as has been pointed out by Porter (1963). Figure 4 shows the leaf morphology, the growth habit, and the phenolic patterns of the four South American species of *Larrea* and of their five natural interspecific hybrids (Hunziker, Palacios, Valesi & Poggio, in preparation). Each species has at least one characteristic marker phenolic compound which is shown by a different type of drawing. These genome marker compounds have been found in the hybrids showing that there is addition of the markers in the hybrids. They have been very helpful for the identification of the parental species of the hybrids (Hunziker *et al.*, in preparation).

All South American species are diploid except *Larrea cuneifolia* which is a tetraploid forming nearly 23 closed bivalents with at least one chiasma at each

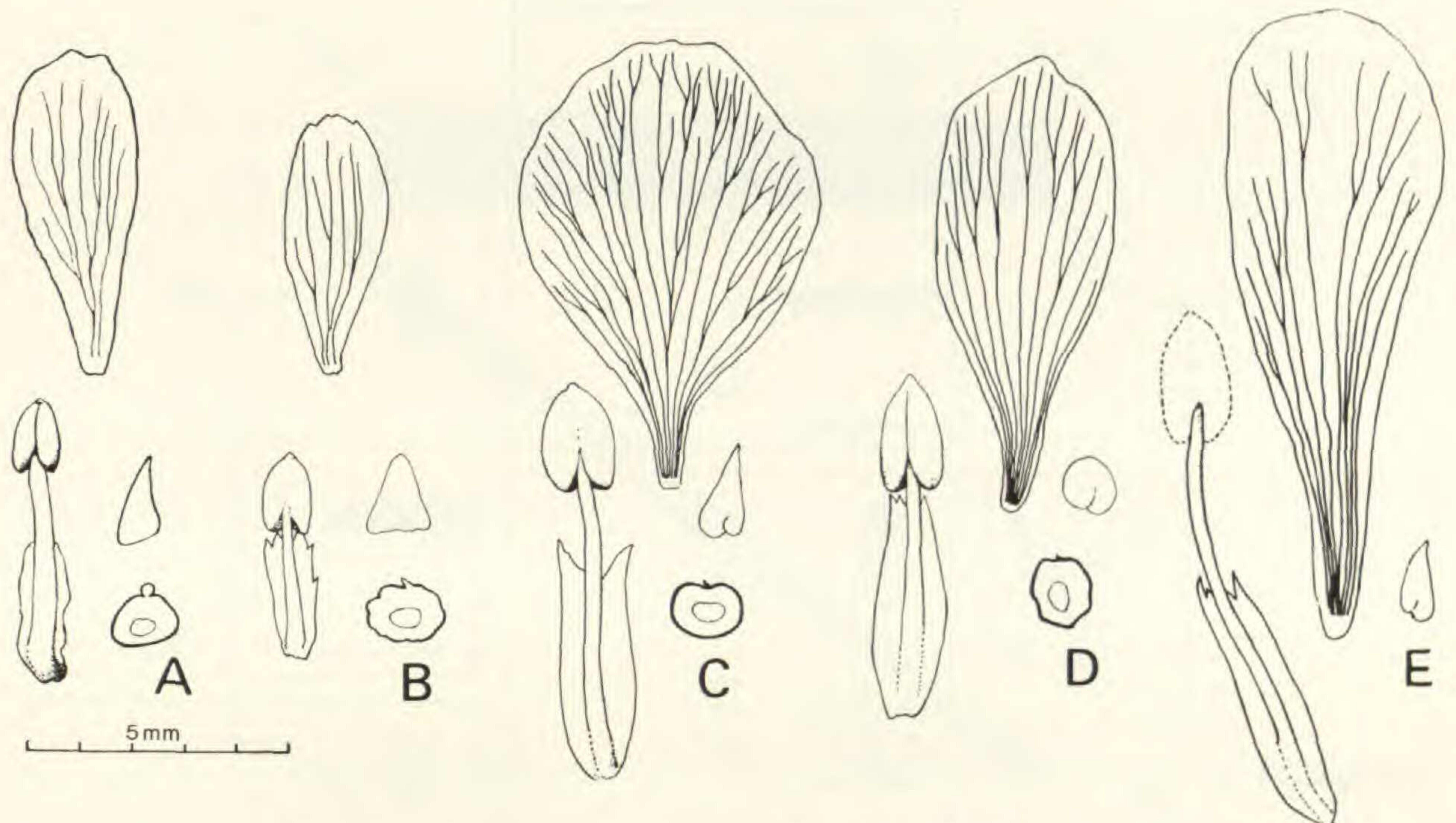


FIGURE 3. Petals, stamens, staminal scales, stipules, and seed cross sections of the five taxa of the genus *Larrea*. A = *L. nitida*, B = *L. ameghinoi*, C = *L. cuneifolia*, D = *L. divaricata* subsp. *divaricata*, E = *L. divaricata* subsp. *tridentata*.

side of the centromere. The diploid South American species form 10.4–12.6 closed bivalents. As the diagram of Fig. 5 indicates, the hybrid *L. ameghinoi* × *L. nitida* is highly fertile and forms nearly 13 bivalents. This points out the close relationship of *L. ameghinoi* to *L. nitida*. It is possible that introgression has occurred between some populations of these two taxa, especially of genes from *L. ameghinoi* to *L. nitida* (Hunziker *et al.*, in preparation).

The triploid hybrid between tetraploid *Larrea cuneifolia* and diploid *L. divaricata*, on the other hand, forms 13 bivalents + 13 univalents in nearly 50% of the

TABLE 1. Leaflet characteristics, chromosome numbers, and geographic distribution of the five taxa of the genus *Larrea*.

Group	Morphological characteristics	Taxon	Leaflet number	Habit	Chromosomes (n)	Distribution
Multifoliolate	Flowers small, mericarps puberulous	<i>L. nitida</i> Cav.	8–16	Erect	13	Argentina and Chile
		<i>L. ameghinoi</i> Speg.	3–7	Prostrate	13	Argentina (Patagonia)
Bifoliolate	Flowers larger, mericarps hairy	<i>L. divaricata</i> Cav. subsp. <i>divaricata</i>	2	Erect	13	Peru, Bolivia Argentina Chile
		<i>L. divaricata</i> Cav. subsp. <i>tridentata</i> (Sesse. & Moc. ex DC.) Felg. & Lowe	2	Erect	13	Chihuahuan Desert
		<i>L. cuneifolia</i> Cav	2	Erect	26	Sonoran Desert
					39	Mohave Desert
					26	Argentina

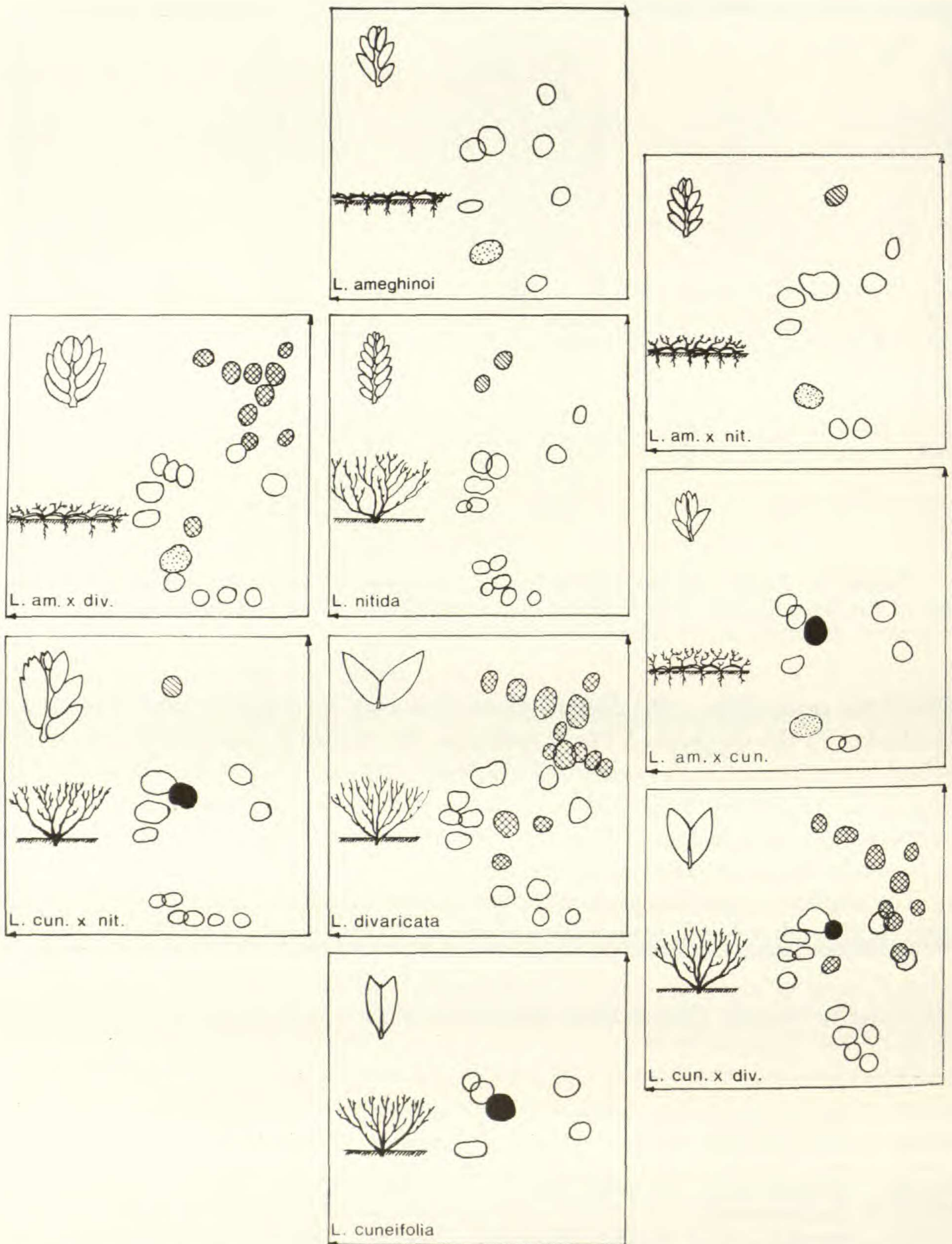


FIGURE 4. Leaves, growth habit, and phenolic compounds of North Patagonian species and hybrids of *Larrea*.

cells (Hunziker *et al.*, in preparation). *Larrea divaricata* is, therefore, one of the parental species of tetraploid *L. cuneifolia* or very closely related to one of the ancestral progenitors. The other hybrids are highly sterile (*L. ameghinoi*  $\times$  *L. cuneifolia*), completely sterile (*L. cuneifolia*  $\times$  *L. divaricata*), or flower rarely and

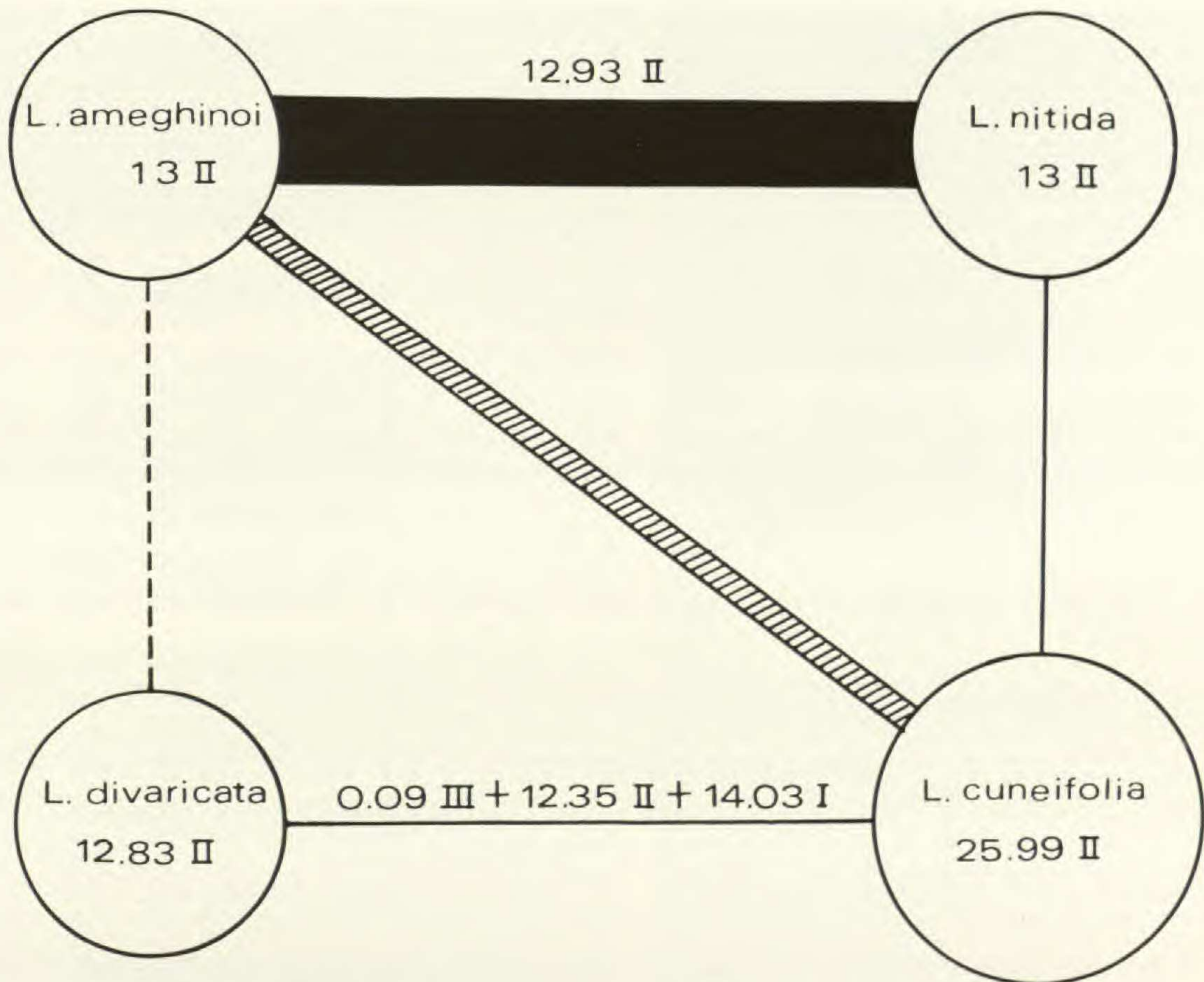


FIGURE 5. Putative crossing relationships of the four species of *Larrea* and their five natural hybrids. Mean chromosome associations are indicated for species and hybrids. The connections between circles give an idea of fertility as measured by the percent of seed-bearing mericarps: black, > 70%; hatched, partially fertile (15–19%); solid line, sterile; broken line, flowering sporadic, almost sterile.

are highly sterile (*L. ameghinoi* × *L. divaricata*). Analysis of chromosome associations in these hybrids could not be studied with success due to the occurrence of cytomixis, which produced cells with very different chromosome numbers and associations.

There is evidence that *L. divaricata* subsp. *tridentata* from California and *L. nitida* or *L. ameghinoi* are self compatible species (Twisselmann, 1956; Raven, 1963; Hunziker *et al.*, in preparation).

*Larrea cuneifolia* is possibly a relatively old species having a fairly wide distribution in Argentina. As we have seen, it shares a genome with *L. divaricata*, which would be one of its diploid progenitors. However, *L. cuneifolia* has lost many of the abundant phenolic markers produced by the South and North American *divaricata* genomes (Figs. 4, 6). The other diploid has apparently become extinct and perhaps was responsible for the two most remarkable morphological characteristics of *L. cuneifolia*: a) the fusion of the leaflets, and b) the orientation of the epiphylls towards the east.

It is probably this last characteristic, which enables the plant to avoid the full exposure of the leaves to noon sunrays, that makes *Larrea cuneifolia* more drought tolerant than *L. divaricata*. Since the *divaricata* diploid genome seems, therefore,

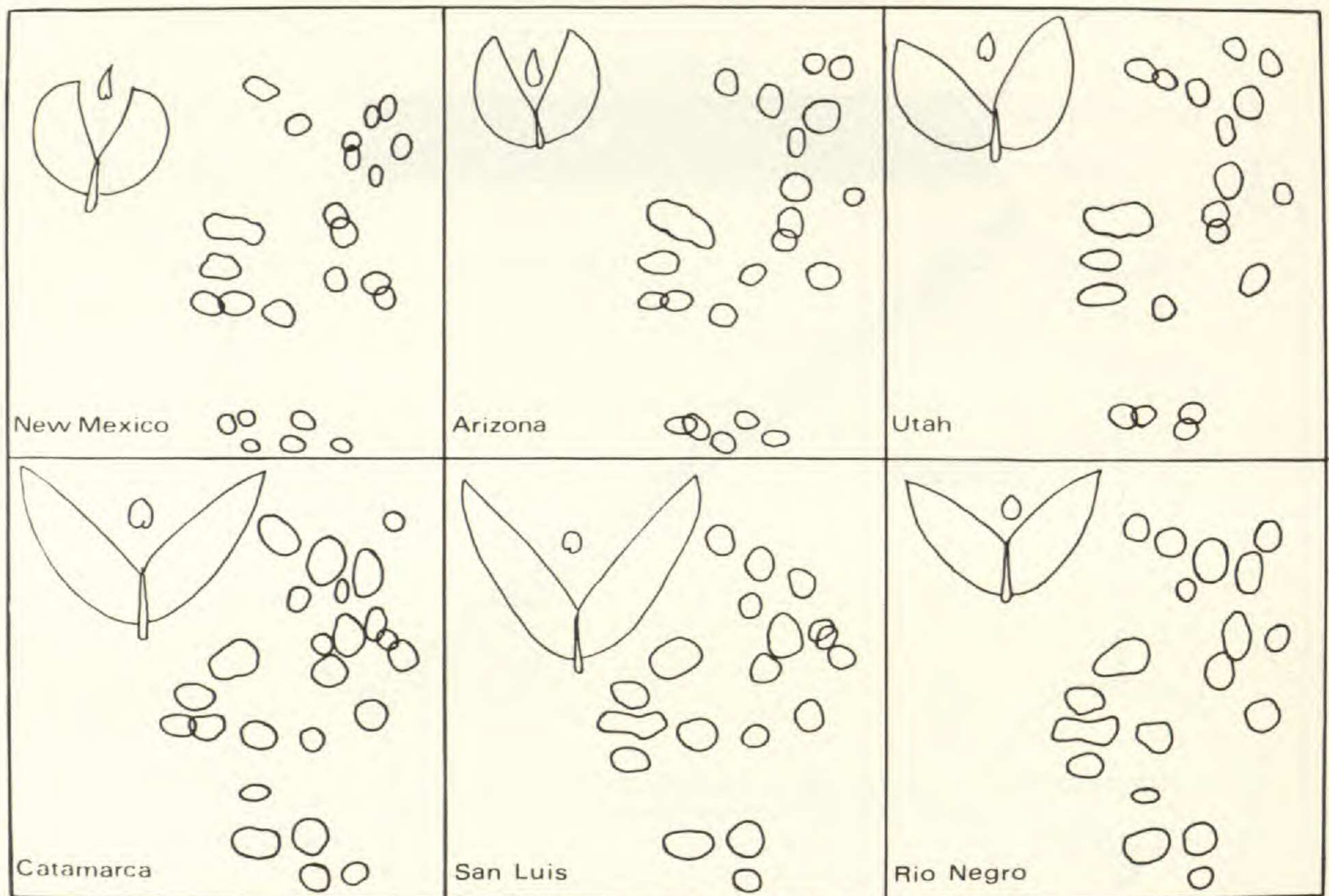


FIGURE 6. Chromatograms and leaf and stipule forms of three populations each of *Larrea divaricata* subsp. *tridentata* (upper row) and *L. divaricata* subsp. *divaricata* (lower row). New Mexico, Eddy Co., diploid (NME); Arizona, Tucson, tetraploid (AP, WA); Utah, near Toquerville, hexaploid (UW). All three collected by Dr. T. W. Yang, who also has determined the chromosome numbers. The samples of *L. divaricata* subsp. *divaricata* are from the northwest (Catamarca Prov., Dep. Belén, near Hualfin), center (San Luis Prov., Luján) and south (Río Negro, Dep. San Antonio, Mina Gonzalito) of Argentina.

to be quite an ancient one in South America it is possible that *L. divaricata* in South America is older than in North America.

#### THE DISJUNCTION OF *LARREA DIVARICATA* AND ITS DIFFERENTIATION IN NORTH AMERICA

The studies of Yang (1970) and Barbour (1969) have shown that *Larrea divaricata* subsp. *tridentata* in North America is composed of 3 races: diploid in the Chihuahuan Desert (Mexico, Texas, New Mexico, Arizona), tetraploid in the Sonoran Desert (Arizona, western Mexico, southeastern California) and hexaploid in the Mohave Desert (California, western Arizona, Nevada, Utah). With a few exceptions, these chromosome races are allopatric.

Yang (1970) studied 41 local races of *Larrea divaricata* subsp. *tridentata* regarding chromosome number. His detailed geographic chromosome survey shows (Fig. 1):

1) There appears to be some sympatric contact in limiting areas of diploids and tetraploids (southeastern Arizona). In some places diploids and tetraploids are living together (Population 18). Also in west-central Arizona and southeastern California hexa- and tetraploid plants occur together.

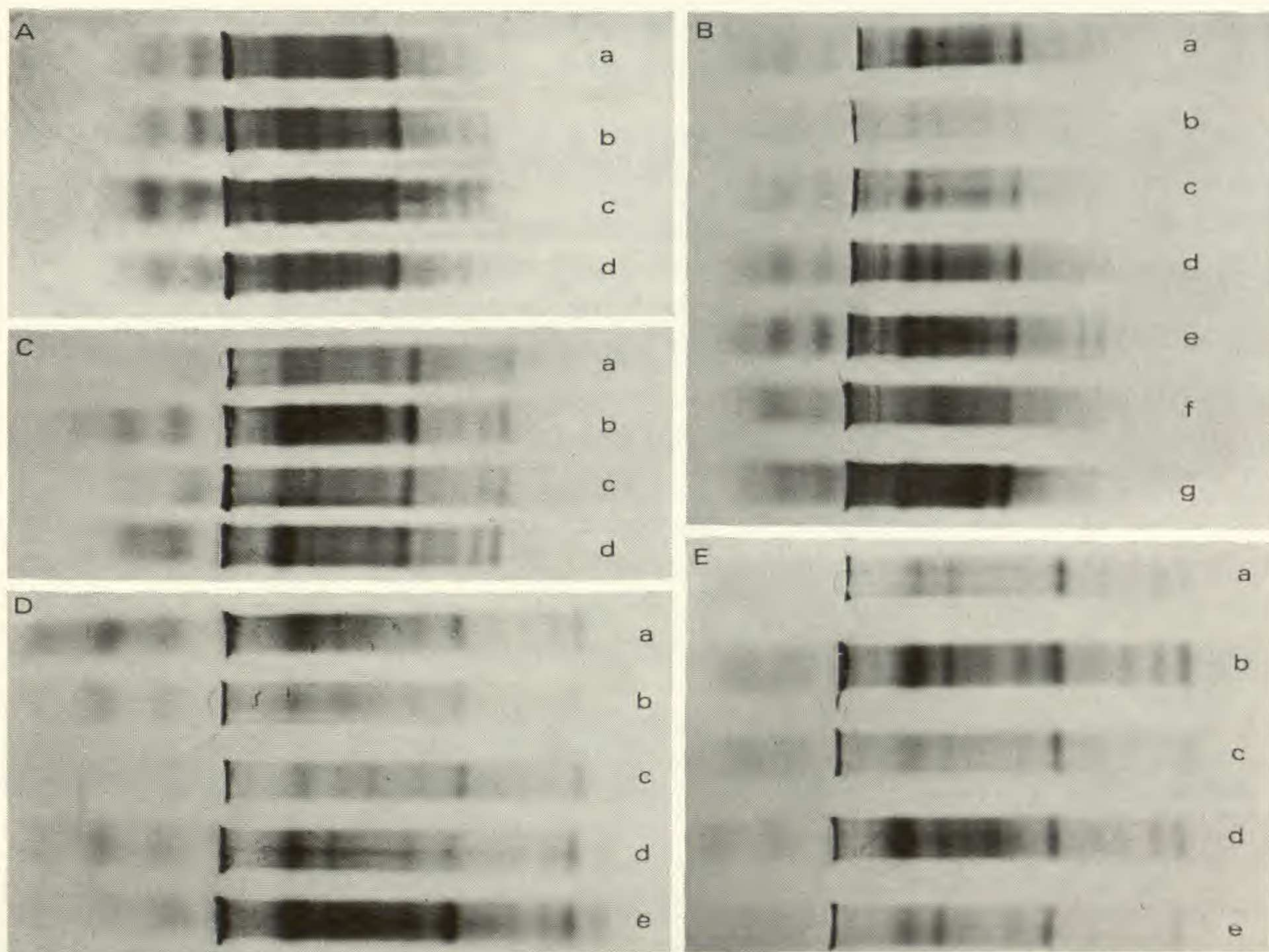


FIGURE 7. Polyacrylamide gel electrophoresis of seed albumins of South and North American *Larrea* species. Anode to the right.—A. Diploid *L. divaricata* from South and North America; a and b = subsp. *divaricata*; c and d = subsp. *tridentata*. [a = Dep. San Antonio, Río Negro, Argentina; b = Dep. Valcheta, 73 km W. of Sa. Grande; c = Hidalgo Co., New Mexico; d = Vizarrón, Querétaro, México.]—B. Diploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A.; a = Arizona, Pima Co.; b = ídem; c = New Mexico, Eddy Co.; d = New Mexico, Luna Co.; e = N. Mexico, Chaves Co.; f = Texas, Maverick Co.; g = Texas, Crockett Co.—C. Tetraploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A. a, b, and c = Arizona, Tucson or vicinity; d = Arizona, Pima Co.—D. Hexaploid *L. divaricata* subsp. *tridentata* from different localities in the U.S.A. a, b = Nevada; c = Nevada, Hoover Dam; d, e = Arizona, Mohave Co.—E. Different polyploid races of *L. divaricata* subsp. *tridentata*. a = diploid, Arizona, Pima Co.; b = tetraploid, Arizona, Pima Co.; c = tetraploid, Arizona, Yuma Co.; d = diploid, New Mexico, Eddy Co.; e = hexaploid, Nevada, Nye Co.

2) In these areas, so far no natural triploids and pentaploids have been found on the basis of actual chromosome counts. This is in fact surprising considering the amount of cross pollination that probably occurs due to insects, and to the fact that in South America hybridization among four different species is frequent and five out of the six possible hybrid combinations have been found. It may be a consequence of the difficulty in distinguishing the parents on morphological grounds. Therefore, the hybrids, if existing, might not be easily detected.

3) Yang (1970) has also found a disjunct diploid in Central Arizona (30 miles north-northeast of population 29, which is tetraploid). It is isolated from tetra-, hexa- and other diploid populations. (The nearest diploids are approximately 100 miles to the southeast.)

4) Diploid and tetraploid populations can be recognized in the field on the



basis of habit, height and other morphological features. Tetra- and hexaploid individuals are more difficult as already mentioned.

On the other hand, several chromosome counts made along a stretch of 2,500 km from individuals collected in the provinces of Salta, Tucumán, Mendoza, and Río Negro (from the northern, western and southern part of the area) indicate that subsp. *divaricata* is uniformly diploid in South America (Fig. 2).

The chromatographic pattern of the phenolics of North and South American specimens of *Larrea divaricata* present some slight differences but on the whole are strikingly similar (Fig. 6).

Electrophoresis of seed albumins has been found to support the arrangement of species within the genus made on morphological grounds (Hunziker, 1971; Hunziker *et al.*, in preparation). Moreover, the electrophoregrams show that there are few differences among diploids of *Larrea divaricata* growing in distant places as northern Patagonia (subsp. *divaricata*) and New Mexico (subsp. *tridentata*); compare *b* and *c* from Fig. 7A, which are separated by 74° latitude or nearly 7,000 km.

Within *Larrea divaricata* subsp. *tridentata* there are not marked differences in the protein patterns of the different chromosomal races. The diploid patterns present some slight differences among themselves (Fig. 7B). There are no obvious differences in the presence or absence of bands among the tetraploids except concentration of certain fractions (Fig. 7C). The hexaploids also show slight variation; they are almost identical except *e*, which shows an extra fast band on the extreme right (Fig. 7D).

As shown in Fig. 7E there are no major differences among di-, tetra- and hexaploid patterns. This strongly suggests that autopolyploidy is involved in the origin of tetra- and hexaploid populations of *Larrea divaricata* subsp. *tridentata*.

If allopolyploidy were involved, the tetra- and hexaploid patterns would be more complex than the diploids because in amphiploids generally there is at least some addition of protein fractions from the original diploids (Hall, 1959; Hall & Johnson, 1962; Johnson & Hall, 1965; Smith *et al.*, 1971).

#### CONCLUSIONS

On the basis of morphological, phenolic, and protein data it is likely that both diploid *Larrea divaricata* from South and North America should be regarded as conspecific, but the final answer to this question should come from the analysis of the hybrid between both populations (chromosome behavior, fertility).

The evidence from morphology, phenolic patterns, and albumin electrophoresis suggests that intervarietal autopolyploidy is involved in the origin, differentiation, and northwest migration of the chromosome races in North America. The entire distribution of the genus, with species diversity in northern Patagonia (primitive and more recent species) and the role played by diploid South American *Larrea divaricata* subsp. *divaricata* in the origin of a relatively old species such as *L. cuneifolia* suggests a South-to-North America pattern of migration. Since *L. divaricata* appears to be self compatible, this characteristic might have helped in the expansion of its range as suggested by Baker (1955).

## LITERATURE CITED

- BAKER, H. G. 1955. Self compatibility and establishment after "long-distance" dispersal. *Evolution* 9: 347-348.
- BARBOUR, M. 1969. Patterns of genetic similarity between *Larrea divaricata* of North and South America. *Amer. Midl. Naturalist* 81: 54-67.
- FELGER, R. S. & C. H. LOWE. 1970. New combinations for plant taxa in northwestern Mexico and southwestern United States. *Jour. Arizona Acad. Sci.* 6: 82-84.
- HALL, O. 1959. Immuno-electrophoretic analyses of allopolyploid rye-wheat and its parental species. *Hereditas* 45: 495-504.
- & B. L. JOHNSON. 1962. Electrophoretic analysis of the amphiploid of *Stipa viridula* × *Oryzopsis hymenoides* and its parental species. *Hereditas* 48: 530-535.
- HUNZIKER, J. H. 1971. El uso simultáneo de datos citogenéticos y moleculares en taxonomía experimental. *En* R. H. Mejía & J. A. Moguilevsky (editors), "Recientes adelantos en biología." Pp. 129-137.
- , R. A. PALACIOS, AMALIA G. DE VALESÍ & LIDIA POGGIO. Hybridization in *Larrea* (Zygophyllaceae): A morphological, cytogenetic and chemosystematic study. (In preparation.)
- JOHNSON, B. & O. HALL. 1965. Analysis of phylogenetic affinities in the Triticinae by protein electrophoresis. *Amer. Jour. Bot.* 52: 506-513.
- MORELLO, J. 1955. Estudios botánicos en las regiones áridas de la Argentina. *Rev. Agron. Noroeste Argentino* 1: 301-370.
- PORTER, D. M. 1963. The taxonomy and distribution of the Zygophyllaceae of Baja California, Mexico. *Contr. Gray Herb.* 192: 99-135.
- RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* 38: 151-177.
- SMITH, H. H., D. E. HARMILL, E. A. WEAVER & K. H. THOMPSON. 1971. Multiple molecular forms of peroxidases and esterases among *Nicotiana* species and amphiploids. *Jour. Hered.* 61: 203-212.
- TWISSELMANN, E. C. 1956. A flora of the Temblor Range and the neighboring part of the San Joaquín Valley. *Wassmann Jour. Biol.* 14: 161-300.
- YANG, T. W. 1970. Major chromosome races of *Larrea divaricata* in North America. *Jour. Arizona Acad. Sci.* 6: 41-45.